INHALING WITHOUT RIBS: THE PROBLEM OF SUCTION IN SOFT-BODIED INVERTEBRATES

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ABSTRACT

Most animals rely upon rigid skeletal structures to withstand the negative pressures required for inhalation. Some soft-bodied invertebrates (innkeeper worms, sea cucumbers) have pumping cloacae that are able to "inhale" without any hard supporting structures. Geometric analyses suggest that inhalation cannot be produced by relaxation of coelomic pressure and contraction of radial muscles connecting the body wall. Coelomic pressure must be maintained for body wall support and radial muscle antagonism. Mathematical models predict that maximum attainable suction in a hydrostatically supported sac-within-a-sac like the cloaca-body wall system will be proportional to coelomic pressure and exponentially related to the ratio of body wall diameter to cloacal diameter. A mechanical model gives results consistent with these predictions. "Cloacal" suctions are proportional to "coelomic" pressure, and maximum suction (20 × coelomic pressure) is produced when the cloaca is small relative to the body wall. *In vivo* recordings of pressure relationships during cloacal pumping in innkeeper worms (*Urechis caupo*) confirm that coelomic pressure is not relaxed to permit inhalation. No animals have been found which use a hydrostatically-supported system to produce extreme suction, with the possible exception of nematodes. Squids apparently utilize the potential of such a mechanism for producing large stroke volumes at low suctions with minimum structural complexity; the mantle is a sac-within-a-sac system which pumps large volumes for respiration and locomotion.

INTRODUCTION

Suction by animals is usually thought to require a rigid framework to support the negative pressure within the animal. The classic example is inhalation in vertebrates. Mammals can inhale because they have a rib cage and a diaphragm. Contraction of the domed diaphragm expands the thoracic cavity, creating negative pressure. The ribs prevent collapse of the walls, and the pressure is equalized by air being drawn into the lungs. A frog cannot inhale directly because it has no rib cage or diaphragm and therefore cannot generate negative pressure in the thoracic cavity. Instead it must use the buccal cavity, which does have a rigid framework and a movable floor, as a pump to inflate the lungs with positive pressure. It appears, then, that a rigid framework with movable elements is a *sine qua non* of suction in vertebrates.

Most sucking invertebrates conform to this generalization. Scorpions, spiders (Parry, 1954), and a few crabs that have been reported to produce suction (Wolcott, 1976; Greenaway & Taylor, 1976) are all arthropods, with rigid exoskeletons. Some invertebrates, though, manage to produce suction in the absence of hard parts.

Notable among these are the holothuroid echinoderms (sea cucumbers) and certain large echiurans (innkeeper worms). These soft-bodied animals use the cloaca as a pump to fill a "water lung" which meets a large proportion of their gas exchange requirements (Winterstein, 1909; Redfield & Florkin, 1931; Bertolini, 1933, Newell and Courtney, 1965).

These animals must produce negative internal pressures to draw in water, but they have no permanent rigid skeleton to support the body wall against collapse. Indeed, their hydrostatic skeleton only provides rigidity if positive internal pressures are maintained. This paper presents a theoretical solution to this apparent paradox and a mechanical model demonstrating the hydrostatics involved. It also compares the theoretical predictions and model performance to the functioning of living cloacal breathers, and comments on the implications for suction among other soft-bodied invertebrates.

Morphology of cloacal pumps

Cloacal breathers share several structural characteristics (Fig. 1). The body wall, although muscular, is intrinsically quite flexible; the animals become limp when dead or anesthetized. The thin-walled, contractile cloaca lies posteriorly in the capacious coelom, connected to the body wall with numerous radial muscles. Posteriorly it opens through the anus; anteriorly it communicates through sphincters with the hindgut and, in the case of sea cucumbers, with the respiratory trees.

A typical respiratory cycle in one of these cloacal breathers consists of three phases: inhalation, lung filling, and exhalation. The mechanisms of lung filling and exhalation are straightforward. Lung filling requires one (Pearse, 1908; Pantin & Sawaya, 1953) to twenty or more (Crozier, 1916; Ogawa, 1928; Tao, 1930) contractions of the cloaca with the anal sphincter closed and the sphincter into the respiratory structure open, forcing cloacal water into the lung. Exhalation involves opening both sets of sphincters and permitting coelomic pressure to collapse the flexible lung, expelling the contents to the exterior.

The mechanism by which the cloaca is refilled so that it may once again pump up the lung is not so obvious. Buddington (1937) hypothesized a two-step ". . . mechanism involved in expansion of the cloaca and thus in the respiratory intake of that organ: 1. General relaxation of the body-wall tissues, including muscles there present, with consequent release of pressure on all organs in the coelom. 2. Active contraction of the numerous separate muscle bundles leading from the cloacal to the body wall." Buddington conceded that his first step is ". . . hardly susceptible of proof on account of the numerous factors involved; but the validity of such assumptions can hardly be doubted since the situation is covered by applying the simplest principles of hydrodynamics." Other workers, although not directly addressing the inhalation question, seem to hold assumptions consistent with Buddington's.

The assumption that cloacal expansion is accomplished by contraction of the radial muscles and relaxation of the body wall presents some difficulties. The radial muscles are anchored to the body wall. Since the body wall is not inherently rigid, it will tend to collapse when the radial muscles contract, unless its distension is maintained by coelomic pressure. An increase in coelomic pressure to antagonize the tension exerted by the radial muscle will, however, increase the hydrostatic force tending to collapse the cloaca. This will require greater tension in the radial muscles, which would appear to require a further increase in coelomic pressure to

prevent collapse of the body wall, and so forth. The cloacal breathers appear to be like the man attempting to lift himself by his bootstraps.

The solution to this apparent paradox lies in the geometry of the animals. The total force preventing collapse of the body wall around the cloaca is equal to the difference between coelomic and ambient pressure times the area of the body wall available for attachment of radial muscles, whereas the total force hindering expansion of the cloaca is the difference between cloacal and the coelomic pressure times the area of the cloaca. One would predict, then, that a net force would be available for expansion of the cloaca if the attachment area of radial muscles on the body wall exceeded the attachment area of those muscles on the cloacal wall. This is indeed the situation in cloacal breathers (Fig. 1), not surprisingly since the cloaca must be smaller in diameter than the body wall enclosing it.

Materials and Methods

The maximum theoretical suction which could be developed by such a hydro-statically-supported "sac-within-a-sac" was calculated as a function of coelomic pressure and body geometry for two simplified body plans. A cylindrical body of indefinite length with a coaxial cloaca (Fig. 2), and a spherical body with a concentric cloaca (Fig. 3), were considered as limiting cases; the geometry of living cloacal breathers lies between these extremes. Several assumptions were made to simplify calculations. The body and cloacal walls were considered infinitely compliant, and effects of tension in the walls therefore disregarded. Static equilibrium was assumed, avoiding frictional and other hydrodynamic effects and allowing the sum of forces across any plane of section to be set at zero.

To test under more realistic conditions the relationships calculated from the mathematical models, a mechanical model with elastic rather than infinitely compliant body walls was constructed. The "cloaca" was a toy balloon, connected by contact-cemented nylon monofilament "radial fibers" to a rubber condom "body wall" (Fig. 4). Cannulae to both "cloacal" and "coelomic" cavities were connected to pressure transducers on a Narco Biosystems polygraph, and to syringes for adjusting cloacal diameter and coelomic pressure. Cloacal pressure was recorded as a function of coelomic pressure at each of several cloacal diameters.
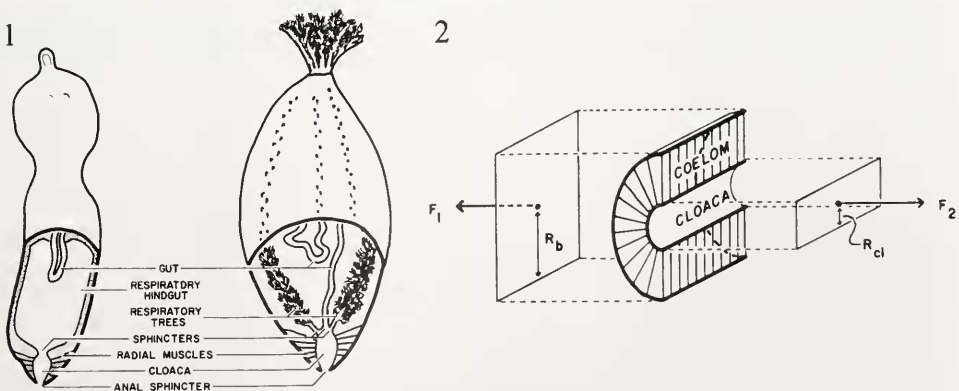

FIGURE 1.   Cloacal pumps. Left: *Urechis caupo* (from life). Right: *Thyone briaereus*, a representative holothuroid (adapted from Hyman after Coe.)

FIGURE 2.   Forces acting on a hydrostatically-supported body composed of coaxial cylinders.
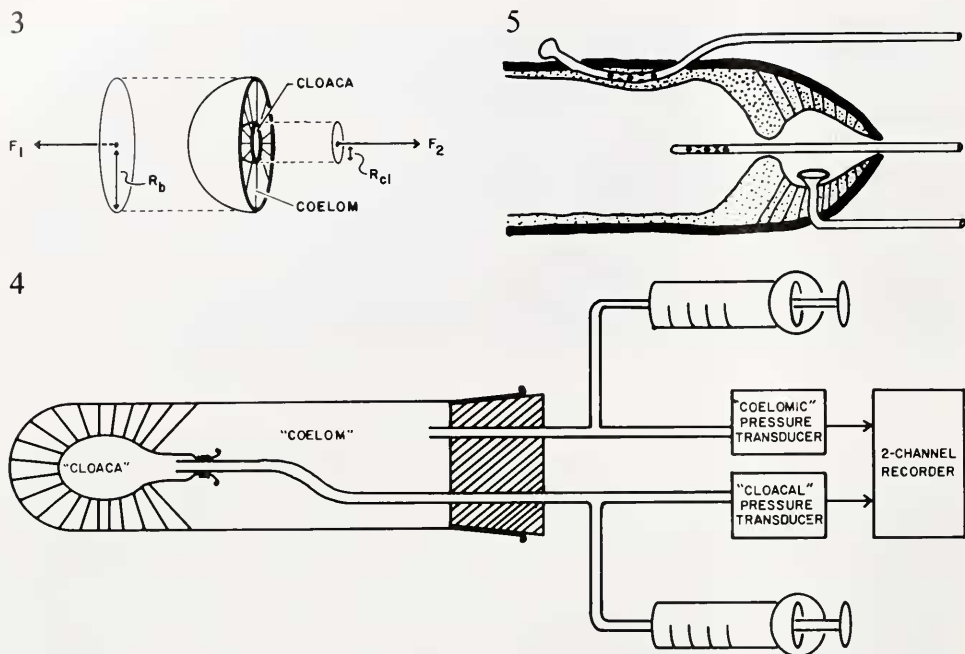
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FIGURE 3. (Upper left) Forces acting on a hydrostatically-supported body composed of concentric spheres.

FIGURE 4. (Bottom) Rubber model of a cloacal pump.

FIGURE 5. (Upper right) Typical catheter placement for obtaining *in vivo* pressure records during cloacal pumping. Top: coelomic. Center: hindgut. Bottom: cloacal.

Experiments with living cloacal breathers were then undertaken to test the predictions based on the theoretical and mechanical models. Specimens of a common holothuroid (*Cacumaria miniata*) and a large (10–15 cm) echiuran (*Urechis caupo*) were obtained from the California coast. The animals were maintained in perforated 500 ml plastic containers in a 15°C recirculating sea water tank. Cannulae were fabricated of Intramedic 7410 polyethylene catheter tubing (Clay-Adams) by heat-forming. Cloacal cannulae were given a 90° bend and a large bell to retain them in the cloaca and bring the tube into line with the animal's axis (Fig. 5). Each coelomic cannula had a large ball melted onto its tip to anchor it, and transverse holes punched about 1 cm back from the tip with a sharpened piece of 25-gauge hypodermic tubing. Cannulae were inserted by thrusting an 18-gauge hypodermic needle through the body wall, threading the cannula through the lumen of the needle, and then withdrawing the needle, leaving the cannula in place. Successful implantation of cloacal cannulae and subsequent clearance from mucus blockage were verified by injecting carmine suspension through the cannula and observing its appearance in exhaled water; coelomic probes in *Urechis* were tested by aspiration of coelomic fluid and observation of pigmented coelomocytes.

Experimental animals were placed in 1-1 dishes of 15°C sea water without restraint other than the cannulae. Coelomic and cloacal pressures were transduced to voltage with LX 1601D hybrid solid-state pressure transducers (National Semiconductor), conditioned by a variable gain/offset preamplifier, and recorded on a two-channel strip chart.

These procedures demonstrated once again that living animals are much less

tractable research subjects than are mathematical models or rubber novelties, and great effort was required to collect useful data from a few successful preparations. The holothuroids consistently expelled their cloacal probes and successfully resisted emplacement of coelomic cannulae. The echiurans clogged their cannulae with mucus, ripped them through the fragile cloacal walls, and spent much effort attempting to rid themselves of the tubing while producing meters of irrelevant pressure records. The extremely thin respiratory hindgut of *Urechis* seemed to hinder accurate reading of coelomic pressures by wrapping around and occluding the holes in the cannula. Therefore, coelomic pressures were also recorded from cannulae threaded through the cloaca into the lumen of the hindgut (Fig. 5); this gave accurate readings but caused such abnormal behavior that little of the data was useful. Ultimately, only "free breathing" pressures were measured since occlusion of the anus triggered writhing, a "cough" reflex, and cessation of normal pumping.

RESULTS

In a cylindrical body plan of indefinite length (Fig. 2) the force F_1 perpendicular to the plane of section and tending to distend the body wall is the pressure differential across the body wall multiplied by the projected area of the body wall on the plane of section: $F_1 = P_{co}2R_bL$; where P_{co} is coelomic pressure referred by ambient, R_b is the body wall radius, and L is length. The force F_2 tending to collapse the cloaca toward the plane of section is the pressure differential across the cloacal wall multiplied by the projected area of the cloaca on the plane of section: $F_2 = (P_{co} - P_{cl}) 2R_{cl}L$; where P_{cl} is cloacal pressure referred to ambient and R_{cl} is cloacal radius. At equilibrium these forces, coupled through the radial fibers, are equal in magnitude but opposite in sign (direction). Thus:

$$P_{co}2R_bL = (P_{co} - P_{cl})2R_{cl}L$$

Cancelling like terms, expanding the right-hand expression, and rearranging terms:

$$P_{cl}R_{cl} = P_{co}R_{cl} - P_{co}R_b$$

Solving for P_{cl}:

$$P_{cl} = P_{co}(1 - (R_b/R_{cl}))$$

In the spherical body plan (Fig. 3) the forces favoring distension are again balanced, equal to the product of pressure differential and projected area of the body wall and cloaca respectively. Thus:

$$P_{co}\pi R_b^2 = (P_{co} - P_{cl})\pi R_{cl}^2$$

Solving for P_{cl} as above:

$$P_{cl} = P_{co}[1 - (R_b/R_{cl})^2]$$

A similar solution would apply for a body plan between the two extremes; the exponent would be determined by the sphericity of the shape and would lie between 1 and 2.

Two relationships are apparent from the above analyses. First, suction attainable in the cloaca is strongly influenced by the relative size of cloaca and body wall, especially in more spherical bodies. As cloacal radius approaches that of the body wall, attainable suction approaches zero (P_{cl} approaches ambient). As cloacal radius decreases, attainable suction rises rapidly and, at cloacal radii smaller than one-half the body radius, exceeds the absolute value of coelomic pressure. The second, and perhaps more striking, relationship is that attainable cloacal suction is directly

proportional to coelomic pressure. If coelomic pressure were released as Buddington (1937) suggested, inhalation would be impossible.

The results obtained with the rubber model (Fig. 6) are entirely consistent with the theoretical predictions. The cloacal suction is clearly proportional to coelomic pressure, and rises strikingly with decreasing cloacal filling (diameter). The suctions attainable at minimum cloacal diameters are remarkable—up to 20 times as large (absolute value) as coelomic pressure. These results again indicate that animals structurally similar to Figure 1 should not relax coelomic pressure during the inhalation stroke of their respiratory cycle. If anything, they might be expected to increase coelomic pressure, particularly if they are forced to suck in water against a pressure gradient. The maximum pressure against which they could suck in water should be related to the ratio of body wall diameter to cloacal diameter.

The pressure relationships in living animals during periods of apparently normal pumping confirm that no general relaxation of coelomic pressure occurs during the inhalation stroke of the respiratory cycle (Fig. 7). There is in fact no correlation between the cloacal and the coelomic pressure cycles, and inhalation may coincide with either a coelomic pressure peak or minimum. Cloacal pressures during inhalation were essentially equal to ambient, since the anus was unrestricted.

DISCUSSION

Both mathematical analyses and the mechanical model indicate that coelomic pressure must be maintained or even increased by contraction of the body wall musculature to produce cloacal suction. Why do *in vivo* recordings show no cor-
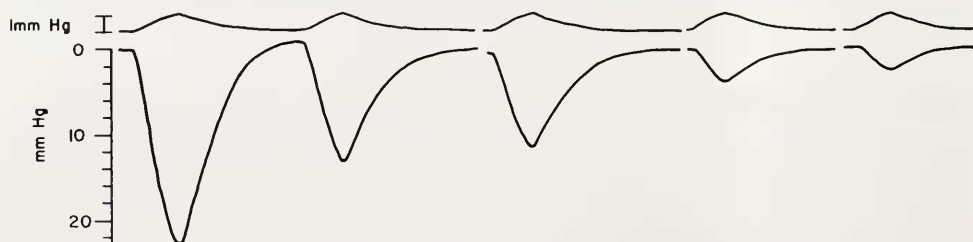

FIGURE 6. "Coelomic" (above) and "cloacal" (below) pressures in the model cloacal pump. Cloacal filling and therefore effective cloacal diameter increase from left to right. Coelomic pressure pulses 1 mm Hg, approx. 30s long.
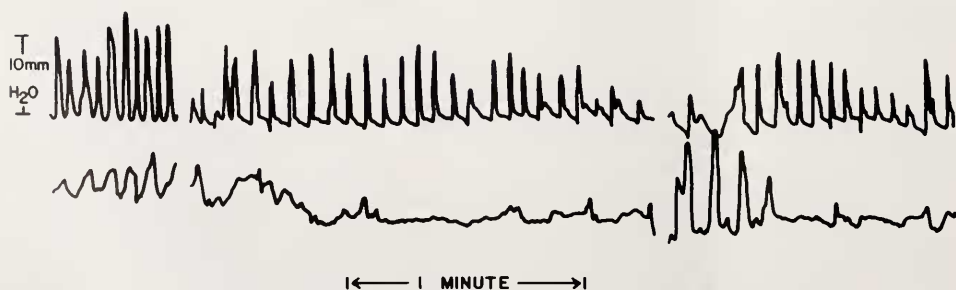

FIGURE 7. Cloacal (upper trace) and coelomic (lower trace) pressures in *Urechis caupo* during cloacal pumping.

relation between cloacal and coelomic pressures? The major reason is presumably that under normal conditions, and under the experimental conditions used, flow into the cloaca through the anus is unrestricted, and very low cloacal suction is required for filling. The increment in coelomic pressure required for radial muscle antagonism is minimal and apparently is masked by the changes in coelomic pressure associated with locomotory and burrow-ventilation movements; it is the latter that give rise to the pronounced rhythms in coelomic pressure in Figure 7. The fact that peaks in coelomic pressure may coincide with inhalation clearly demonstrate that relaxation of the body wall is not necessary for cloacal expansion. Indeed, such relaxation hinders pumping, as predicted. Some of the animals occasionally expelled all of the hindgut respiratory water and became completely flaccid. When they recommenced pumping, dimpling and collapse of the body wall at the points of radial muscle attachment were clearly evident, and cloacal filling was poor until enough hindgut volume had been accumulated to make the hydrostatic skeleton effective once again, confirming that adequate coelomic pressure is necessary for effective suction in *Urechis*.

This may not be the case in sea cucumbers, despite their architectural similarity to *Urechis*. It has long been known that sea cucumbers, while extremely limp when anesthethized or dead, are capable of rendering the connective tissue of the body wall quite rigid (Jordan, 1914, 1919). The facultative alteration of viscoelastic properties, an apparently unique property of echinoderm connective tissue, is caused by alteration of the ionic composition in the tissue matrix (Eylers, 1976; Wilkie, 1978) and gives the cucumber the ability to produce a semi-rigid exoskeleton, under nervous control and independent of coelomic pressure. Given the low suctions required for normal cloacal breathing, it is unnecessary to postulate a hydrostatic mechanism for supporting negative cloacal pressures in these animals, although such a mechanism may contribute to the process.

The mathematical analyses indicate that animals with a ratio of body wall diameter to cloacal diameter greater than 2:1 could theoretically produce cloacal suctions of greater magnitude than the coelomic pressure supporting the hydrostatic system. The mechanical model demonstrates that with appropriate body geometry a soft-bodied invertebrate could generate suction at least an order of magnitude greater than the coelomic pressure. The capabilities of the hydrostatic system appear to far exceed the minimal suctions required for cloacal pumping, and it is tempting to seek other animals in which the potential of such a system is more fully exploited. One group in which the ability to produce high suction would appear useful is the sand-eating deposit feeders like the hemichordate *Balanoglossus aurantiacus* or the polychaete lugworm *Arenicola marina*, both of which ingest remarkable quantities of sand. Wet sand is virtually impossible to push into a tube; however, suction will draw interstitial water into the tube, entraining an almost solid plug of sand. The requirements of these worms thus seem well matched to the capabilities of a hydrostatically-supported suction mechanism. Nevertheless, neither of them has the appropriate structure, and each uses a different technique for ingesting sand: ciliary action in enteropneusts (Barrington, 1940; Knight-Jones, 1953); proboscis eversion in *A. marina* (Jacobsen, 1967).

Nematodes are another group which relies on a hydrostatic skeleton and characteristically feeds by suction. In this case the structural similarities between the nematode buccal region and the *Urechis* cloacal region are somewhat more pronounced if the pharyngeal bulb is construed as a sac-within-a-sac separated by copious radial muscle, and it may be quite reasonable to invoke similar mechanisms for producing suction. Verification of such an hypothesis would present considerable

difficulty, due to the small size of the cavities in which pressure would have to be monitored.

With the possible exception of the nematodes, then, no group of soft-bodied invertebrates seems to use a hydrostatically-supported mechanism for the production of high suction. It may be that development of these mechanisms has reached an evolutionary dead end—those animals that might find its capabilities advantageous do not possess the requisite morphology, while those which do have the structures have no need to fully exploit the potential high-suction capability of the system.

Although production of high suction requires a large ratio of body-wall radius to suction-cavity radius, a hydrostatically supported system also can produce low suctions with suction-cavity radii nearly as large as the body wall radius. In other words, if the pressure required is low, the stroke volume can be a substantial proportion of the total body volume. This property is exploited in the mantle of the squid, for jet propulsion as well as respiration. Large quantities of water are drawn in through wide inhalent openings and then expelled at high velocity through the narrow funnel; a complete cycle in *Loligo* may require less than 0.5 s (Ward, 1972). The mantle consists of an external and internal tunic, between which lie alternating bands of circular muscle fibers and radial muscle fibers connecting the two tunics (Ward and Wainwright, 1972). Water is expelled by rapid, synchronous contraction of the circular fibers. The mechanism by which the mantle is re-expanded has been the subject of some discussion; Ward (1972) dismisses positive-pressure pumping and Bernoulli effects, proposing that thinning of the mantle wall by contraction of the radial muscles must cause an increase in circumference, since the mantle does not lengthen and the volume of muscle tissue presumably does not decrease.

This mechanism for expansion of the squid mantle is a sac-within-a-sac system functionally identical with the cloacal pump of *Urechis*. The inner tunic corresponds to the cloaca, the outer tunic to the body wall, and the muscle layer (when the circular fibers are relaxed) behaves like a fluid within the observed range of deformation (20–30%; Ward, 1972). The suction potential of the mantle structure is slightly more than 10% of the hydrostatic pressure in the muscle layer (calculated by substituting measurements from Ward, 1972, in the above equation describing cylindrical animals). This potential suction is presumably well above what is required to draw in water through the unrestricted inhalent openings, although no pressure records from the mantle cavity or muscle layer are available. The hydrostatically-supported suction system permits the squid to produce only moderate suction, but more importantly it allows large stroke volume and rapid pumping through the mantle cavity without complex supporting structures that might interfere with streamlining, and without accessory pumps and valves that would introduce delays and additional fluid friction.

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